Microb Ecol
DOI 10.1007/s00248-011-9973-x

ENVIRONMENTAL MICROBIOLOGY

# Fungal Community Composition in Neotropical Rain Forests: the Influence of Tree Diversity and Precipitation

**Krista L. McGuire · Noah Fierer · Carling Bateman · Kathleen K. Treseder · Benjamin L. Turner**

Received: 30 May 2011 / Accepted: 20 October 2011


**Abstract** Plant diversity is considered one factor structuring soil fungal communities because the diversity of compounds in leaf litter might determine the extent of resource heterogeneity for decomposer communities. Lowland tropical rain forests have the highest plant diversity per area of any biome. Since fungi are responsible for much of the decomposition occurring in forest soils, understanding the factors that structure fungi in tropical forests may provide valuable insight for predicting changes in global carbon and nitrogen fluxes. To test the role of plant diversity in shaping fungal community structure and function, soil (0–20 cm) and leaf litter (O horizons) were collected from six established 1-ha forest census plots across a natural plant diversity gradient on the Isthmus of Panama. We used 454 pyrosequencing and phospholipid fatty acid analysis to evaluate correlations between microbial community composition, precipitation, soil nutrients, and plant richness. In soil, the number of fungal taxa increased significantly with increasing mean annual precipitation, but not with plant richness. There were no correlations between fungal communities in leaf litter and plant diversity or precipitation, and fungal communities were found to be compositionally distinct between soil and leaf litter. To directly test for effects of plant species richness on fungal diversity and function, we experimentally re-created litter diversity gradients in litter bags with 1, 25, and 50 species of litter. After 6 months, we found a significant effect of litter diversity on decomposition rate between one and 25 species of leaf litter. However, fungal richness did not track plant species richness. Although studies in a broader range of sites is required, these results suggest that precipitation may be a more important factor than plant diversity or soil nutrient status in structuring tropical forest soil fungal communities.

K. L. McGuire (✉) · C. Bateman
Barnard College, Columbia University,
3009 Broadway,
New York, NY 10027, USA
e-mail: kmcguire@barnard.columbia.edu

C. Bateman
e-mail: carling.bateman@gmail.com

N. Fierer
University of Colorado,
Boulder, CO, USA
e-mail: noah.fierer@colorado.edu

K. K. Treseder
University of California,
Irvine, CA, USA
e-mail: treseder@uci.edu

B. L. Turner
Smithsonian Tropical Research Institute,
Apartado 0843-03092,
Balboa, Ancon, Republic of Panama
e-mail: turnerbl@si.edu

## Introduction

Soil fungi are integral components to nutrient cycling in forest ecosystems [1], but little is known about the ecological factors that structure their diversity and distribution in tropical rain forests. While several recent studies in tropical rain forests have used DNA sequencing technologies to assess microbial diversity [2–5], our knowledge of tropical soil fungi is mostly limited to sporocarp surveys and community profiling data [6–8]. Most molecular-based investigations of soil fungi have been performed in temperate and boreal systems (e.g., [9–11]), but the unique attributes of tropical ecosystems mean it might not be possible to generalize findings from higher latitudes to soil microbes in tropical forests [12].

Published online: 12 November 2011

Lowland tropical rain forests often contain hundreds of tree species per hectare [13, 14], which may have important implications for soil fungi involved in litter decomposition. Leaf structure, chemistry, and elemental stoichiometry vary markedly across plant taxa, and the quantity and quality of plant-derived organic inputs can influence decomposition rates [15–18]. Fungi degrade a large portion of the plant-derived compounds [19], so the diverse mixtures of leaf litter on the forest floor of tropical rain forests may enable the coexistence of diverse fungal taxa via resource partitioning [20, 21]. Spatial differentiation and resource partitioning has been demonstrated for several groups of fungi [22–24], indicating that resource heterogeneity may be important for supporting diverse fungal assemblages. Nonetheless, field and laboratory experiments evaluating links between plant diversity, fungal diversity, and ecosystem function have yielded mixed results [1, 25, 26]. Furthermore, the few studies that have been performed in tropical ecosystems have been conducted in experimental, montane, or agricultural systems (e.g., [27–29]). Therefore, the applicability of those results to diverse lowland rain forest is unknown.

In this study, we evaluated the effects of plant litter diversity on fungal diversity and function using a series of plots in tropical rain forest across the Isthmus of Panama that varied in tree diversity [30]. Findings from the natural diversity gradient were integrated with experimental manipulations of plant diversity in a litter decomposition experiment. We tested the hypotheses that (1) fungal diversity and microbial biomass would be positively correlated with natural gradients in plant diversity and (2) fungal diversity would be correlated with experimental manipulations of leaf litter diversity, mimicking patterns found across the natural plant diversity gradient.

## Methods

### Field Work

To assess the effects of natural variations in plant diversity, we examined soil fungal diversity and microbial biomass in pre-existing plots in Panama that contained between 63 and 165 tree species $ha^{-1}$. All plots were 1 ha in size and characterized as old growth, primary forest [30]. These plots also varied in mean annual precipitation and several soil properties (Table 1), so all quantified biotic and abiotic factors were included in the final analyses. From each plot, 15 composite soil cores (0–20 cm) were collected from random locations within each plot. At the same point of soil core collection, the leaf litter (O horizons) from the forest floor was also collected, as we expected that fungi in freshly fallen and partially decomposed litter might respond differently to plant diversity and precipitation compared to fungi in mineral soil. Following field collection, samples were immediately frozen at −20 °C. In addition to microbial analyses (see following section), soils were analyzed for pH in a 1:2 water ratio using a glass electrode and Mehlich P, Ca, K, Mg, Al, Fe, Mn, and Zn using inductively coupled plasma atomic emission spectroscopy [31]. To generate C/N ratios, total C and N were analyzed using dry combustion.

To directly test for effects of plant species richness on fungal diversity and function, we experimentally re-created litter diversity gradients in 2-mm nylon screen litter bags (20×20 cm) with 1, 25, and 50 species of plant leaf litter. Leaf litter was collected in traps on Barro Colorado Island over a period of 6 months (emptied every week), air-dried, and identified to species when possible. Plant species were randomly selected from a pool of 72 species (supplementary docs) and placed in three separate combinations for each treatment. For single species treatments, we selected *Doliocarpus* sp. (Dilleniaceae), *Trichilia tuberculata* (Meliaceae), and *Alseis blackiana* (Rubiaceae) because these species were abundant in litter traps and are well represented in a 50-ha permanent forest research plot that has been intensely studied since 1980 [32]. Leaf litter was manually broken into pieces for every treatment in order to fit all species combinations into the litter bags. Litter bags were filled with 15 g of leaf litter for each treatment and placed on the mineral soil surface in three sites in the primary rain forest on Barro Colorado Island outside of the 50-ha research plot. All three of the litter decomposition sites were of the same soil type (AVA soil; Typic Eutrudox [33]) and had similar mean annual precipitation. After 6 months, bags were collected and weighed to determine the effect of plant litter diversity on mass loss rates.

### Microbial Analyses

DNA was extracted from 0.25 g sub-samples of the composite soil and litter samples in each plot and from each litter bag using the Powersoil DNA extraction kit (MoBio, Carlsbad, CA, USA). Three DNA extractions from each sample were pooled to obtain a better representation of the microbial community [34]. General fungal primers targeting the fungal 18S rRNA gene [35] were modified and successfully implemented to amplify the general fungal community using a barcoded pyrosequencing procedure described previously [36–39]. The forward primer consisted of the 454 Life Sciences Primer B attached to the SSU817f primer with an "AG" linker sequence (GCCTTGCCAGCCCGCTCAGAGTTAGCATGGAA TAATRR-AATAGGA). The reverse primer contained the 454 Life Sciences Primer A, a unique 12 base-code barcode for each PCR product, with an "AC" sequence linking it to the SSU1196r primer (GCCTCCCTCGCGCCATCAG-12 bp barcode ACTCTGGACCTGGTGAGTTTCC). The 12-bp bar-

**Table 1** Data for plots used in microbial analyses that naturally varied in plant diversity and other biotic and abiotic factors (plant data from Pyke et al. [30])

| | Plot ID | | | | | |
|---|---|---|---|---|---|---|
| | 7 | B3 | B1 | B6 | 9 | 32 |
| Annual ppt (mm) | 2,438 | 2,579 | 2,589 | 2,589 | 2,889 | 3,293 |
| # Species | 93 | 99 | 84 | 76 | 107 | 165 |
| Fisher's alpha | 39.21 | 41.59 | 31.41 | 23.1 | 41.6 | 81.35 |
| Shannon (*H'*) | 3.96 | 3.97 | 3.53 | 2.66 | 3.91 | 4.52 |
| pH | 4.5 | 6.4 | 6.3 | 5.6 | 4.9 | 5.8 |
| P (mg $Pkg^{-1}$) | 2.1 | 1.5 | 3.6 | 7.0 | 1.5 | 1.3 |
| Al (mg Al $kg^{-1}$) | 745.5 | 791.7 | 1,302.8 | 1,396.3 | 886.5 | 968.4 |
| Total bases (Ca+K+Mg) | 387.9 | 3,285.7 | 2,111.2 | 1,046.5 | 2,297.0 | 2,057.9 |
| $NH_4$ (mg $Nkg^{-1}$) | 0.3 | 1.7 | 2.4 | 2.3 | 4.8 | 2.5 |
| $NO_3$ (mg $Nkg^{-1}$) | 1.8 | 2.9 | 2.3 | 2.5 | 1.0 | 1.6 |
| C/N ratio | 6.7 | 8.0 | 8.5 | 8.9 | 5.1 | 10.4 |

All data for plant communities were derived from woody species ≥10.0 cm dbh. Soils analyses were derived from mineral soil cores (0–20 cm)

code allowed us to pool together all of the amplicons for sequencing with sequences ultimately assigned to individual samples. Amplifications were done according to a previously described protocol [36] using 0.25 μl of each primer (30 mM), 3 μl of DNA template, and 22.5 μl Platinum PCR SuperMix (Invitrogen, Carlsbad, CA, USA). Fungal amplicons were sequenced on a Roche 454 Gene Sequencer at the Environmental Genomics Core Facility at the University of South Carolina (Columbia, SC, USA) running the titanium chemistry.

Following pyrosequencing, sequences were processed through the Quantitative Insights Into Microbial Ecology (QIIME) pipeline [40]. In QIIME, sequences were quality checked, aligned, and grouped into phylotypes at a 97% sequence similarity cutoff. While 97% sequence similarity is an arbitrary delineation of fungal taxa, other ecological studies use this and similar cutoff values (e.g., [2, 11, 41]). One phylotype representative from each group was chosen, and a phylogenetic tree was constructed with the FastTree algorithm [42]. The closest taxonomic identity for each representative phylotype was determined by BLAST comparison against sequences contained within the SILVA database [43] and GenBank.

Microbial biomass was measured on plot samples of soil and leaf litter using phospholipid fatty acid analysis (PLFA). PLFA was not performed on litter bag samples, as there was insufficient material. For PLFA analyses, two samples (2 g each) of both organic and mineral soil were lyophilized from each plot [44]. Lipids were extracted from each sample with a single-phase, phosphate-buffered, $CHCl_3$–$CH_3OH$ solvent and separated from neutral and glycolipid fractions by silicic acid column chromatography. Phospholipids were transesterified to fatty acid methyl esters and quantified by mass spectrometry [45, 46] using an Agilent 6980N gas chromatography system (Agilent Technologies). Total PLFAs were used as an index of living microbial biomass. The mean for both PLFA extractions was used in the calculations for each sample.

### Statistical Analyses

To determine the relationships between fungal community composition (fungal phylotypes and total biomass), plant species richness, soil chemistry, and mean annual precipitation across the 1-ha plots, Spearman rank correlation analyses were performed using SPSS (SPSS v. 17.0 for Mac, Chicago, IL, USA). Compositional differences in fungal communities across soil and litter horizons were analyzed by analysis of similarity (ANOSIM). Data were rarified to 1,000 sequences prior to downstream analyses. Proportional counts of rarified phylotypes were then square-root transformed minimizing the influence of rare taxa. Nonmetric multidimensional scaling plots were used to visualize similarity in fungal community composition across plots (Primer v6).

For the litter bag decomposition experiment, a general linear model was used to evaluate the effects of litter diversity on fungal richness. Spearman rank correlation analyses were used to test for relationships between fungal richness, plant litter richness, and decomposition rate (*k*).

## Results

### Plot Analyses

Four hundred fifty-four pyrosequencing yielded a total of 57,560 sequences with 9,733 phylotypes and an average of 1,598 sequences per sample. Seventeen percent were non-fungal eukaryotes and 0.4% could not be identified to

**Table 2** Results of Spearman ranked correlations for fungal taxa and microbial biomass in litter, mineral soil, and both horizons combined

| | | Plant richness Spearman's $\rho$ | Precipitation Spearman's $\rho$ |
|---|---|---|---|
| | Total fungal phylotypes (litter) | 0.40 | 0.10 |
| | Total fungal phylotypes (soil) | 0.39 | 0.75* |
| | Total fungal phylotypes (litter+soil) | 0.41 | 0.57* |
| | Total microbial biomass (litter+soil) | 0.38 | 0.10 |
| Litter | Total fungal orders | 0.30 | −0.20 |
| | Total fungal families | −0.30 | 0.00 |
| | Total microbial biomass | 0.31 | 0.09 |
| Soil | Total fungal orders | 0.52 | 0.74* |
| | Total fungal families | 0.37 | 0.90** |
| | Total microbial biomass | 0.54 | 0.99** |

$N$=12; one soil and one litter sample were analyzed per plot

*$p$<0.05; **$p$<0.01

domain. Prior to statistical analyses, non-fungal and unclassifiable sequences were removed, leaving an average of 945 sequences per sample and 367 unique phylotypes per sample (soil and litter samples were counted separately).

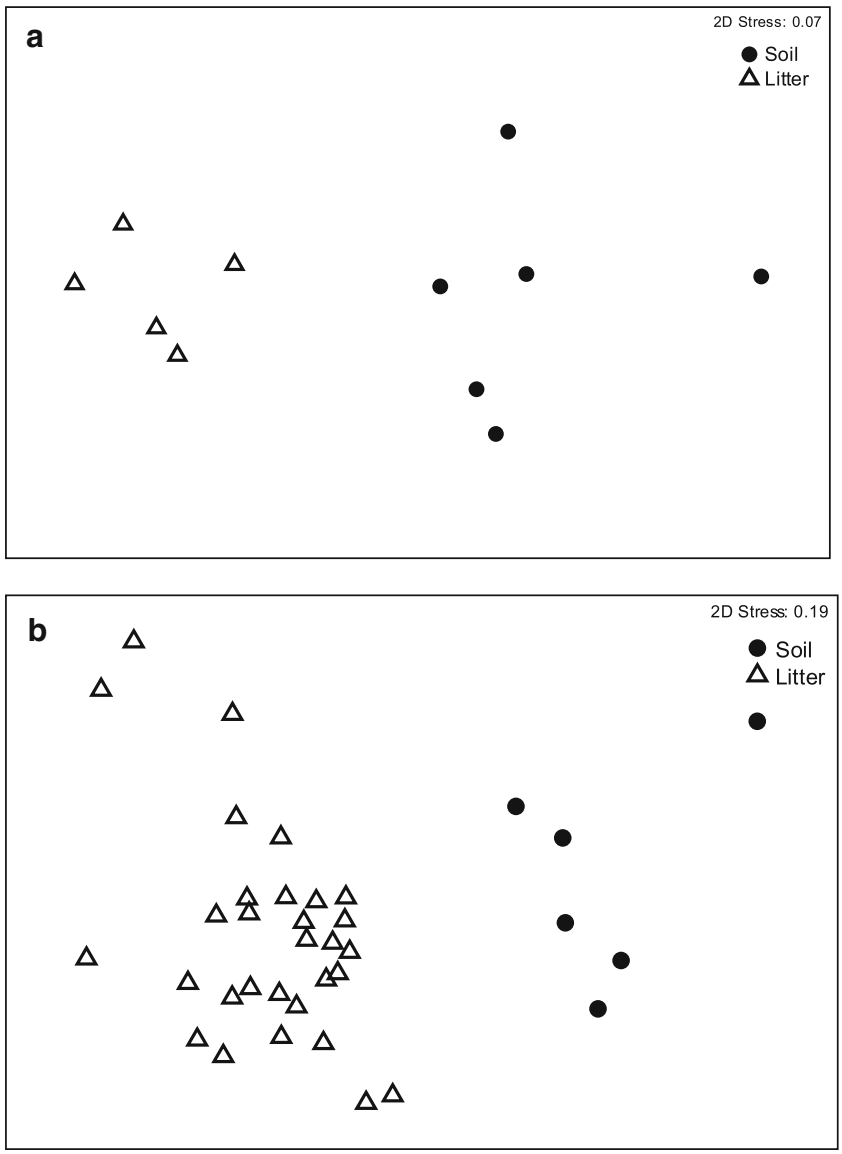


**Figure 1** Nonmetric multidimensional scaling plots showing compositional separation of fungal communities across litter (O horizons; $N$=5) and mineral soil ($N$=6) horizons for plots (**a**) and all samples including litter bags (**b**) ($N$=36)

Across plots, the total number of fungal phylotypes (soil+litter) was not significantly correlated with plant species richness but was significantly correlated with mean annual precipitation (Table 2). When analyzed separately, soil and litter fungi responded differently to precipitation; total soil fungal phylotypes increased significantly with increasing mean annual precipitation, whereas precipitation had no significant effect on litter fungi (Table 2).

When separated out by soil vs. litter horizons, ANOSIM showed that fungal communities were distinct across horizons (Fig. 1; $R$=0.96, $p$<0.001). In soils, there were significantly more fungal sequences from the *Chytridiomycota* (Fig. 2; $F$ (1, 10)=16.1; $p$=0.003) and *Glomeromycota* ($F$ (1, 10)=15.8; $p$=0.003). By contrast, litter samples contained significantly more *Ascomycota* ($F$ (1, 10)=9.9; $p$=0.01). Total *Basidiomycota* sequences did not differ significantly among soils ($F$ (1, 10)=1.5; $p$=0.2).

Total microbial biomass (per gram of dry matter) showed similar patterns across horizons as pyrosequencing results: Microbial biomass was significantly correlated with mean annual precipitation in soil samples ($\rho$=0.81, $p$<0.03), but not with plant richness or stem number (Table 2). Microbial biomass was not significantly correlated with any of the plant metrics or precipitation in litter or when data for soil and litter samples were combined. In soils, the mole percentage of the 16:1$\omega$5$c$ PLFA, an indicator of arbuscular mycorrhizal biomass [47, 48], was significantly correlated with mean annual precipitation ($\rho$=0.81, $p$=0.03) and tree species richness ($\rho$=0.78; $p$=0.04). The mole percentage of fungal biomass in litter was significantly correlated with the number of tree stems ($\rho$=0.77; $p$=0.04), but not with any other plot metric. Total microbial biomass per gram of dry matter was significantly higher in litter compared to soil samples ($F$ (1, 10)=46.9, $p$<0.001), and the mole percentage of fungal PLFAs was also significantly higher in litter

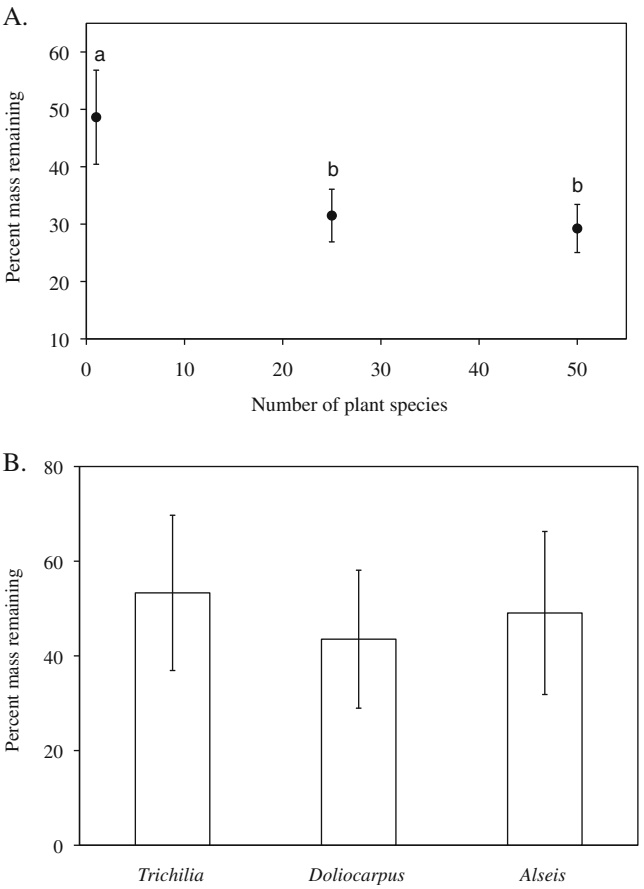


**Figure 3** Percent mass remaining in leaf litter bags ($N$=26) for all species treatments (**a**) and for single species treatments (**b**) after 6 months (mean ±SE). *Different letters above error bars* indicate significance at $p$<0.05

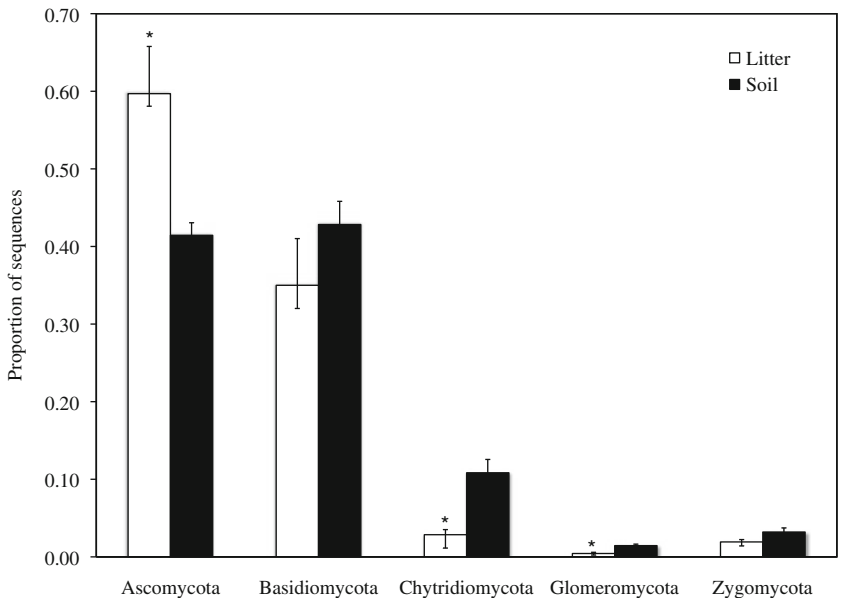


**Figure 2** Relative abundances of fungal phyla found in litter ($N$=5) versus soil ($N$=6) fractions of 1-ha plots. For each sample, abundances were calculated as the proportion of sequences in each fungal phylum. *Asterisks* indicate significance at $p$<0.05

versus soil samples ($F$ (1, 10)=29.6, $p$<0.001), resulting in higher fungal to bacterial ratios in litter ($F$ (1, 10)=23.0, $p$< 0.001).

Soil elemental analyses (Table 1) revealed that in soil samples, total microbial biomass was positively correlated with total inorganic N ($\rho$=0.77, $p$=0.04) but none of the other elemental data. $NH_4$ was positively correlated with total fungal phylotypes ($\rho$=0.77, $p$=0.02) and total fungal families ($\rho$=0.83, $p$=0.02). C/N ratios were positively correlated with total fungal orders ($\rho$=0.94, $p$=0.002).

### Litter Bag Experiment

After 6 months, decomposition of leaf litter in single species bags was significantly slower than decomposition in 25 ($p$=0.03) and 50 species treatments (Fig. 3a; $p$=0.02). However, there was no difference in decomposition rates between 25 and 50 species treatments ($p$=0.96). There was also no difference in decomposition rates among single species litter bags containing only *Doliocarpus* sp., *Trichilia*, or *Alseis* (Fig. 3b).

Fungal richness was not significantly correlated with plant litter diversity. In single species treatments, fungal communities decomposing *Doliocarpus* sp. litter were significantly clustered (Fig. 4; $R$=0.94), but there were no detectable patterns in fungal communities for other single species litter bags.

## Discussion

We found little support for the hypothesis that increasing the number of leaf litter species decomposing on the forest floor will result in greater diversity and abundance of fungal communities. There was also no relationship among plant richness and fungal richness in the 1-ha forest plots, indicating that relationships among fungal diversity and the plant species in these forests are complex with no clear pattern of correlation. Rather, our results from 454 pyrosequencing showed that soil fungal richness was positively correlated with increasing precipitation, but not with increasing tree species richness or soil nutrients. However, since we only analyzed samples from six 1-ha plots, results should be interpreted with caution, as more intensive sampling across the precipitation gradient may reveal different correlates of soil fungal communities.

The fact that there was not a clear relationship between fungal diversity and plant diversity is counter to expectations, particularly in the litter decomposition experiment. Based on our results, the observed increase in decomposition rates from one to 25 litter species in the litter bag experiment did not appear to result from parallel increases in fungal richness. Numerous studies have reported additive and synergistic effects of litter mixing in decomposition experiments [1, 49], and microbial community composition has been suggested as a plausible mechanism for these patterns [25, 50]. However, relationships between plant diversity, microbial diversity, and ecosystem function have been highly variable across studies [51, 52], and we only found significant relationships between litter diversity and decomposition at the low end of the plant litter richness continuum. Other experiments have found similar results, in which a decelerating relationship between decomposition rates and increasing microbial or plant litter species was observed [53–55]. This type of relationship between diversity and function implies some level of functional overlap among decomposer microbes in their breakdown of plant materials [53]. More detailed chemical analyses of the

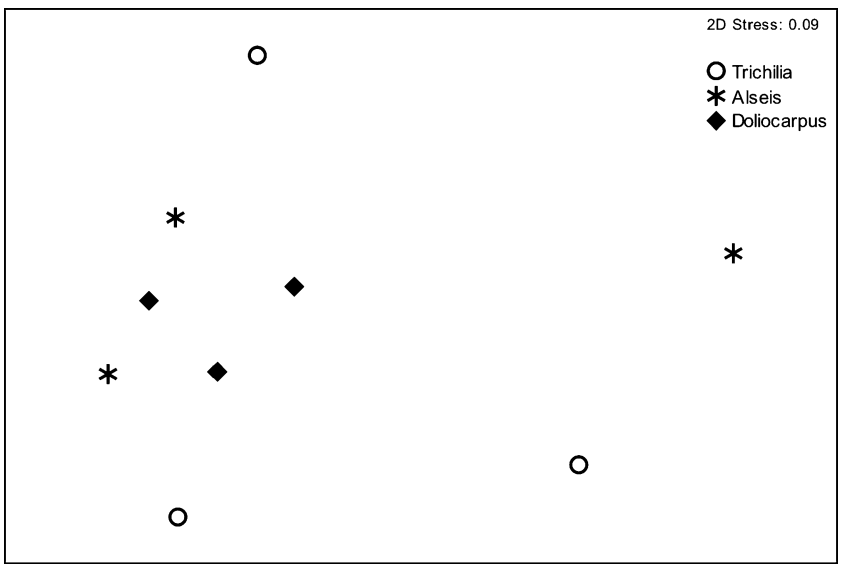


**Figure 4** Non-metric multidimensional scaling plot of fungal communities in single species litter bag treatments ($N$=9). There was no overall difference in fungal communities between the three litter types; however, fungal communities in bags with *Doliocarpus* litter were more similar to each other (ANOSIM $p$<0.05) when samples were coded as *Doliocarpus* vs. non-*Doliocarpus*

plant litter we used in the decomposition experiment may reveal that the plant species were more similar chemically than would be expected taxonomically [56]. Focusing on the litter chemistry, rather than the plant species composition per se, should be a priority for future studies.

Our results showing that fungal richness increases at the high end of the precipitation gradient are different from a recent manipulative rainfall study in California [57] and another experimental study in an old-field ecosystem [58]. In the California study, fungal diversity was the highest under low rainfall treatments [57], and in the old-field experiment, fungal abundance was not affected by precipitation; however, fungal community composition was altered, although the responses were lineage-specific [58]. The manipulative nature of these experiments may account for the differences we observed across the gradient on the Isthmus of Panama, as the experimental studies would capture short-term dynamics, whereas climatic gradients result from the accumulation patterns and processes integrated over centuries or longer. An alternative and more likely explanation for the disparate patterns is that it may not be possible to generalize the findings from coastal grasslands and old-field ecosystems to tropical rain forests, particularly since mean annual precipitation ranges are much higher in Panama than in coastal grasslands and old-field communities. There may also be annual variations and seasonal patterns that were not accounted for in our single time point collections [59].

Across all samples, we found that fungal communities were distinct in litter versus soil, indicating vertical segregation of microbial communities across these horizons. Organic horizons contain greater quantities of labile sugars and higher C/N ratios than deeper soil horizons [19, 60], which may facilitate the proliferation of decomposer taxa that are more competitive for these C substrates. Other studies in boreal and temperate ecosystems have detected vertical segregation of fungi [11, 23, 61] and differences in microbial biomass [62], suggesting broad generalizability of this pattern. Whether or not the taxa found in litter vs. deeper horizons are functionally similar across ecosystems remains to be tested. In addition to distinctive community composition, fungi in litter versus mineral soil horizons showed different relationships to plant richness and precipitation. It is difficult to draw strong inferences from the data, as many of these fungal groups have not been extensively studied, particularly in the tropics. Nonetheless, this study highlights the potential importance of precipitation as an abiotic factor structuring fungal communities and is one of the first studies to evaluate these relationships in lowland tropical rain forests.

**Acknowledgments** We thank Joe Wright and Osvaldo Calderon for collection and identification of all litter species in the decomposition experiment. Collecting and export permits were granted from the Autoridad Nacional del Ambiente of Panama. Jenny Talbot and Angela Nguyen assisted with C and N measurements, and Steve Allison and Donovan German helped with extracellular enzyme assays and data interpretation. We also thank two anonymous reviewers for helping to improve the quality and clarity of the manuscript. This work was funded by NSF Ecosystems (DEB-0640666) and the Kearney Foundation.

## References

1. Hattenschwiler S, Tiunov AV, Scheu S (2005) Biodiversity and litter decomposition in terrestrial ecosystems. Annu Rev Ecol Evol Syst 36:191–218
2. McGuire KL, Zak DR, Edwards IP, Blackwood CB, Upchurch R (2010) Slowed decomposition is biotically mediated in an ectomycorrhizal, tropical rain forest. Oecologia 164:785–795
3. Peay KG, Kennedy PG, Davies SJ, Tan S, Bruns TD (2010) Potential link between plant and fungal distributions in a dipterocarp rainforest: community and phylogenetic structure of tropical ectomycorrhizal fungi across a plant and soil ecotone. New Phytol 185:529–542
4. Tedersoo L, Nilsson RH, Abarenkov K, Jairus T, Sadam A, Saar I, Bahram M, Bechem E, Chuyong G, Koljalg U (2010) 454 Pyrosequencing and Sanger sequencing of tropical mycorrhizal fungi provide similar results but reveal substantial methodological biases. New Phytol 188:291–301
5. Fierer N, Jackson RB (2006) The diversity and biogeography of soil bacterial communities. Proc Natl Acad Sci U S A 103:626–631
6. Watling R (2001) The relationships and possible distributional patterns of boletes in South-East Asia. Mycol Res 105:1440–1448
7. Lindblad I (2001) Diversity of poroid and some corticoid wood-inhabiting fungi along the rainfall gradient in tropical forests, Costa Rica. J Trop Ecol 17:353–369
8. Lodge DJ (1997) Factors related to diversity of decomposer fungi in tropical forests. Biodivers Conserv 6:681–688
9. Buee M, Reich M, Murat C, Morin E, Nilsson RH, Uroz S, Martin F (2009) 454 Pyrosequencing analyses of forest soils reveal an unexpectedly high fungal diversity. New Phytol 184:449–456
10. Taylor DL, Herriott IC, Stone KE, McFarland JW, Booth MG, Leigh MB (2010) Structure and resilience of fungal communities in Alaskan boreal forest soils. Can J For Res-Rev Can Rech For 40:1288–1301
11. O'Brien HE, Parrent JL, Jackson JA, Moncalvo JM, Vilgalys R (2005) Fungal community analysis by large-scale sequencing of environmental samples. Appl Environ Microbiol 71:5544–5550
12. Powers JS, Montgomery RA, Adair EC, Brearley FQ, DeWalt SJ, Castanho CT, Chave J, Deinert E, Ganzhorn JU, Gilbert ME, Gonzalez-Iturbe JA, Bunyavejchewin S, Grau HR, Harms KE, Hiremath A, Iriarte-Vivar S, Manzane E, de Oliveira AA, Poorter L, Ramanamanjato JB, Salk C, Varela A, Weiblen GD, Lerdau MT (2009) Decomposition in tropical forests: a pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. J Ecol 97:801–811
13. Gentry AH (1992) Tropical forest biodiversity—distributional patterns and their conservational significance. Oikos 63:19–28
14. Valencia RH, Balslev H, Paz H, Mino CG (1994) High tree alpha-diversity in Amazonian Ecuador. Biodivers Conserv 3:21–28
15. Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79:439–449
16. Couteaux MM, Bottner P, Berg B (1995) Litter decomposition, climate and litter quality. Trends Ecol Evol 10:63–66

17. Perez-Harguindeguy N, Diaz S, Cornelissen JHC, Vendramini F, Cabido M, Castellanos A (2000) Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. Plant Soil 218:21–30
18. Sariyildiz T, Anderson JM (2002) Interactions between litter quality, decomposition and soil fertility: a laboratory study. Soil Biol Biochem 35:391–399
19. Berg B, McClaugherty C (2003) Plant litter: decomposition, humus formation, carbon sequestration. Springer, Berlin
20. McGuire KL, Bent E, Borneman J, Majumder A, Allison SD, Treseder KK (2010) Functional diversity in resource use by fungi. Ecology. doi:10.1890/09-0654
21. Hanson CA, Allison SD, Bradford MA, Wallenstein MD, Treseder KK (2008) Fungal taxa target different carbon sources in forest soil. Ecosystems 11:1157–1167
22. Boddy L (1999) Saprotrophic cord-forming fungi: meeting the challenge of heterogeneous environments. Mycologia 91:13–32
23. Dickie IA, Xu B, Koide RT (2002) Vertical niche differentiation of ectomycorrhizal hyphae in soil as shown by T-RFLP analysis. New Phytol 156:527–535
24. Genney DR, Anderson IC, Alexander IJ (2006) Fine-scale distribution of pine ectomycorrhizas and their extramatrical mycelium. New Phytol 170:381–390
25. Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setala H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35
26. Jonsson LM, Nilsson MC, Wardle DA, Zackrisson O (2001) Context dependent effects of ectomycorrhizal species richness on tree seedling productivity. Oikos 93:353–364
27. Carney KM, Matson PA (2006) The influence of tropical plant diversity and composition on soil microbial communities. Microb Ecol 52:226–238
28. Waldrop MP, Balser TC, Firestone MK (2000) Linking microbial community composition to function in a tropical soil. Soil Biol Biochem 32:1837–1846
29. Ushio M, Wagai R, Balser TC, Litayama L (2008) Variations in the soil microbial community composition of a tropical montane forest ecosystem: does tree species matter? Soil Biol Biochem 40:2699–2702
30. Pyke CR, Condit R, Aguilar S, Lao S (2001) Floristic composition across a climatic gradient in a neotropical lowland forest. J Veg Sci 12:553–566
31. Turner BL, Romero TE (2009) Short-term changes in extractable inorganic nutrients during storage of tropical rain forest soils. Soil Sci Soc Am J 73:1972–1979
32. Leigh EG, Loo de Lao S, Condit R, Hubbell SP, Foster RB, Pérez R (2004) Barro Colorado Island forest dynamics plot, Panama. In: Losos EC, Leigh EG (eds) Tropical forest diversity and dynamism: findings from a large-scale plot network. The University of Chicago Press, Chicago, pp 451–463
33. Dieter D, Elsenbeer H, Turner BL (2010) Phosphorus fractionation in lowland tropical rainforest soils in central Panama. Catena 82:118–125
34. Feinstein LM, Sul WJ, Blackwood CB (2009) Assessment of bias associated with incomplete extraction of microbial DNA from soil. Appl Environ Microbiol 75:5428–5433
35. Borneman J, Hartin RJ (2000) PCR primers that amplify fungal rRNA genes from environmental samples. Appl Environ Microbiol 66:4356–4360
36. Fierer N, Hamady M, Lauber CL, Knight R (2008) The influence of sex, handedness, and washing on the diversity of hand surface bacteria. Proc Natl Acad Sci U S A 105:17994–17999
37. Lauber CL, Hamady M, Knight R, Fierer N (2009) Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. Appl Environ Microbiol 75:5111–5120
38. Hamady M, Walker JJ, Harris JK, Gold NJ, Knight R (2008) Error-correcting barcoded primers for pyrosequencing hundreds of samples in multiplex. Nat Methods 5:235–237
39. Rousk J, Baath E, Brookes PC, Lauber CL, Lozupone C, Caporaso JG, Knight R, Fierer N (2010) Soil bacterial and fungal communities across a pH gradient in an arable soil. ISME J 4:1340–1351
40. Caporaso JG, Kuczynski J, Stombaugh J, Bittinger K, Bushman FD, Costello EK, Fierer N, Pena AG, Goodrich JK, Gordon JI, Huttley GA, Kelley ST, Knights D, Koenig JE, Ley RE, Lozupone CA, McDonald D, Muegge BD, Pirrung M, Reeder J, Sevinsky JR, Tumbaugh PJ, Walters WA, Widmann J, Yatsunenko T, Zaneveld J, Knight R (2010) QIIME allows analysis of high-throughput community sequencing data. Nat Methods 7:335–336
41. Allison SD, McGuire KL, Treseder KK (2010) Resistance of microbial and soil properties to warming treatment seven years after boreal fire. Soil Biol Biochem 42:1872–1878
42. Price MN, Dehal PS, Arkin AP (2009) FastTree: computing large minimum evolution trees with profiles instead of a distance matrix. Mol Biol Evol 26:1641–1650
43. Pruesse E, Quast C, Knittel K, Fuchs BM, Ludwig WG, Peplies J, Glockner FO (2007) SILVA: a comprehensive online resource for quality checked and aligned ribosomal RNA sequence data compatible with ARB. Nucleic Acids Res 35:7188–7196
44. White DC, Stair JO, Ringelberg DB (1997) Quantitative comparisons of in situ microbial biodiversity by signature biomarker analysis. J Ind Microbiol 17:185–196
45. Bligh EG, Dyer WJ (1954) A rapid method of total lipid extraction and purification. Can J Biochem Physiol 37:911–917
46. Zelles L (1999) Fatty acid patterns of phospholipids and lipopolysaccharides in the characterisation of microbial communities in soil: a review. Biol Fertil Soils 29:111–129
47. van Diepen LTA, Lilleskov EA, Pregitzer KS, Miller RM (2007) Decline of arbuscular mycorrhizal fungi in northern hardwood forests exposed to chronic nitrogen additions. New Phytol 176:175–183
48. Olsson PA (1999) Signature fatty acids provide tools for determination of the distribution and interactions of mycorrhizal fungi in soil. FEMS Microbiol Ecol 29:303–310
49. Gartner TB, Cardon ZG (2004) Decomposition dynamics in mixed-species leaf litter. Oikos 104:230–246
50. Chapman SK, Newman GS (2010) Biodiversity at the plant–soil interface: microbial abundance and community structure respond to litter mixing. Oecologia 162:763–769
51. Andren O, Balandreau J (1999) Biodiversity and soil functioning—from black box to can of worms? Appl Soil Ecol 13:105–108
52. Zak DR, Holmes WE, White DC, Peacock AD, Tilman D (2003) Plant diversity, soil microbial communities, and ecosystem function: are there any links? Ecology 84:2042–2050
53. Bell T, Newman JA, Silverman BW, Turner SL, Lilley AK (2005) The contribution of species richness and composition to bacterial services. Nature 436:1157–1160
54. Setala H, McLean MA (2004) Decomposition rate of organic substrates in relation to the species diversity of soil saprophytic fungi. Oecologia 139:98–107
55. Wohl DL, Arora S, Gladstone JR (2004) Functional redundancy supports biodiversity and ecosystem function in a closed and constant environment. Ecology 85:1534–1540
56. Meier CL, Bowman WD (2008) Links between plant litter chemistry, species diversity, and below-ground ecosystem function. Proc Natl Acad Sci U S A 105:19780–19785

57. Hawkes CV, Kivlin SN, Rocca JD, Huguet V, Thomsen MA, Suttle KB (2010) Fungal community responses to precipitation. Glob Chang Biol 17:1637–1645
58. Castro HF, Classen AT, Austin EE, Norby RJ, Schadt CW (2010) Soil microbial community responses to multiple experimental climate change drivers. Appl Environ Microbiol 76:999–1007
59. Baath E, Soderstrom B (1982) Seasonal and spatial variation in fungal biomass in a forest soil. Soil Biol Biochem 14:353–358
60. Trumbore S (2000) Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. Ecol Appl 10:399–411
61. Lindahl BD, Ihrmark K, Boberg J, Trumbore SE, Hogberg P, Stenlid J, Finlay RD (2007) Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. New Phytol 173:611–620
62. Fierer N, Schimel JP, Holden PA (2003) Variations in microbial community composition through two soil depth profiles. Soil Biol Biochem 35:167–176